



The Afrotropical ponerine ant genus *Asphinctopone* Santschi (Hymenoptera: Formicidae)

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Abstract

The Afrotropical ponerine ant genus *Asphinctopone* is revised. Two species are recognised, of which one (*differens*) is described as new, and two names are established as new junior synonyms of the type-species *silvestrii* (*lucidus* and *lamottei*). A new diagnosis of the genus is presented, based on the female castes (male remains unknown) and critical morphological characters are discussed.

Key words: *Asphinctopone*, taxonomy

Introduction

Asphinctopone is one of the most rarely collected and least known small ponerine genera of the Afrotropical region. Specimens are seldom found and most samples recovered consist of only one or two workers. As a measure of its rarity, a survey of leaf litter in Ghana (Belshaw & Bolton, 1994) recorded 43,824 individual ants, of which only 5 (about 0.01%) were *Asphinctopone*. Despite this rarity, the genus is widespread in wet forest zones in leaf litter, topsoil, pieces of rotten wood and rotting vegetation on the forest floor. One worker has been found foraging in a fallen, abandoned termitary (Dejean *et al.*, 1996). Beyond this nothing is known of its biology. Its specialised morphology implies that it may be prey-specific, but in reality its victims remain unknown.

The genus is a member of subfamily Ponerinae, tribe Ponerini, as diagnosed by Bolton (2003). Within the tribe the morphology of *Asphinctopone* appears to imply that it belongs in the currently confused mass of genus-group names that surrounds *Pachycondyla* and its synonyms, but a recent molecular study (Ouellette, Fisher & Girman, 2006) relates it to *Odontomachus* (for morphology see Brown, 1976). Whichever turns out to be correct, the present analysis makes it clear that *Asphinctopone* is a valid genus, isolated from either possibility by several important characters.

Measurements and indices

All measurements are in millimetres.

Total Length (TL)	The total outstretched length of the ant from the mandibular apex to the gastral apex.
Head Length (HL)	The length of the head capsule excluding the mandibles, measured in full-face view in a straight line from the midpoint of the anterior clypeal margin to the midpoint of the posterior margin.

Head Width (HW)	The maximum width of the head behind the eyes, measured in full-face view.
Cephalic Index (CI)	HW divided by HL, $\times 100$.
Scape Length (SL)	The maximum straight-line length of the scape, excluding the basal constriction or neck.
Scape Index (SI)	SL divided by HW, $\times 100$.
Ocular Index (OI)	Maximum diameter of eye divided by HW, $\times 100$.
Pronotal Width (PW)	The maximum width of the pronotum in dorsal view.
Weber's Length (WL)	The diagonal length of the mesosoma in profile, from the point at which the pronotum meets the cervical shield to the posterior basal angle of the metapleuron.

Abbreviations of depositories

AMNH	American Museum of Natural History, New York, New York, U.S.A.
ANIC	Australian National Insect Collection, Canberra, Australia.
BMNH	The Natural History Museum (= British Museum, Natural History), London, U.K.
CASC	California Academy of Sciences, San Francisco, California, U.S.A.
DEUN	Dipartimento de Entomologia e Zoologia Agraria "Filippo Silvestri", Università di Napoli, Italy.
LACM	The Natural History Museum of Los Angeles County, Los Angeles, California, U.S.A.
MCZC	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.
MNHN	Museum National d'Histoire Naturelle, Paris, France.
MSNM	Museo Civico di Storia Naturale, Milano, Italy.
NHMB	Naturhistorisches Museum, Basel, Switzerland.

Genus *Asphinctopone*

Asphinctopone Santschi

Asphinctopone Santschi, 1914: 318. Type-species: *Asphinctopone silvestrii* Santschi, 1914: 318, by monotypy.

Lepidopone Bernard, 1953: 207. Type-species: *Lepidopone lamottei* Bernard, 1953: 208, by monotypy. [Synonymy with *Asphinctopone* by Brown, 1953: 2.]

Diagnosis of worker and queen (gyne)

- 1 Mandible with 5 teeth; sometimes with an additional denticle between teeth 4 and 5.
- 2 Mandible oblique, not triangular; without a basal pit; with a weakly developed basal groove.
- 3 Masticatory margin of mandible somewhat oblique so that there is a gap between the mandibles basally when they are closed.
- 4 Basalmost tooth is at the rounded basal angle; basal margin shallowly convex; *near the articulation the inner margin with a small tooth-like process* (overlapped by anterolateral angles of clypeal lobe when mandibles closed).
- 5 Palp formula 3,3; second maxillary palpomere elongate and slender.
- 6 *Clypeus complex: in full-face view the median portion projects anteriorly as a broad lobe which terminates in a distinct angle on each side; these angles overlap the basal margins of the mandibles; the anterior clypeal margin has a small median rounded projection, on each side of which the anterior margin is shallowly concave; above the median projection the central portion of the clypeus forms a narrow ridge to the frontal lobes.*

- 7 Frontal lobes small, closely approximated, with only a linear median impression between them; in full-face view anterior margins of frontal lobes are behind anterior margin of clypeus.
- 8 Antenna with 12 segments, gradually incrassate apically and the terminal three segments form a weak club; *apical antennomere hypertrophied, longer than the five preceding segments together*.
- 9 Promesonotal suture deeply impressed, cross-ribbed on extreme anterior mesonotum; metanotal groove deeply impressed and cross-ribbed; mesonotum conspicuously isolated by these two impressions (worker only).
- 10 Mesopleuron with a transverse suture that divides it into anepisternum and katepisternum.
- 11 Metapleural gland orifice simple, posterolateral.
- 12 Propodeal spiracle very small, its sclerite almost circular but the orifice itself a small ellipse.
- 13 Propodeal lobes very reduced, rounded.
- 14 Mesosternal and metasternal processes present, the former narrowly bidentate, the latter narrowly bilobate and very long.
- 15 Mesotibiae and metatibiae each with a single pectinate spur.
- 16 Dorsal (outer) surfaces of middle and hind tibiae and basitarsi without cuticular spines or peg-like traction setae.
- 17 Pretarsal claws small and simple.
- 18 Petiole surmounted by a high, unarmed scale that is narrow in profile and broad in dorsal view.
- 19 Subpetiolar process complex: in profile with a short anterior prominence, a small submedian tooth and a posterior flange.
- 20 Sternite of petiole in posterior view complex (see discussion below).
- 21 *Helcium with a narrow transverse crest of cuticle between the ventral apices of the tergal arch* (see discussion below).
- 22 Prora present, long in profile, broad in anterior view with a thick outer annulus and a deep central concavity; prora in profile projects anteriorly to about the midlength of the helcium (see discussion below).
- 23 *Gastral segment 2 (abdominal segment IV) without trace of differentiated presclerites on tergum or sternum*.
- 24 Gastral tergite 2 (abdominal tergite IV) without a stridulitrum.
- 25 Queen (gyne) only: fractionally larger than the worker and with 3 ocelli present (absent in workers). Mesosoma with full complement of flight sclerites.

Discussion of characters

The characters in *italics* above are considered autapomorphic for the genus. Some of the other characters are probably also apomorphies of which analogues have apparently developed convergently elsewhere in tribe Ponerini. Some of these are discussed below. Characters that involve disarticulation or dissection are from *silvestrii*. Only the holotype of *differens* is known and it has not been dissected, so the presence of character 21 awaits confirmation in that species.

1 Most *silvestrii* workers had five teeth on each mandible, but in two workers examined the left mandible had the usual 5 teeth while the right mandible had an additional denticle present between teeth 4 and 5. Conversely, one worker had 5 teeth plus a denticle on the right mandible and 5 teeth on the left. The holotype of *differens* has 6 teeth on the left mandible (right overlapped and not visible), of which the second tooth is low and rounded, probably through wear.

4 The second part of this characterisation appears autapomorphic. Nothing matching it has yet been observed elsewhere in Ponerini.

5 Palp formula is not 4,4, as was erroneously recorded in Bolton (2003).

8 The apical antennomere is conspicuously elongated but is not markedly broader than the preapical. Its relative length is greater in *Asphinctopone* than in any other Ponerini.

15 Members of the *Pachycondyla* group of Ponerini genera, and of *Odontomachus*, almost universally have two spurs on the mesotibia and two on the metatibia. In each case the anterior spur is small and simple to barbate, the posterior spur is larger and pectinate.

19 Subpetiolar process in ventral view shows a blunt prominence anteriorly, from which arises a pair of short, divergent carinae that extend posteriorly and terminate in a small tooth on each side just in front of the midlength (appearing single in absolute profile). Posterior to this the remainder of the sternite forms a curved plate that terminates in a posteroventrally directed elevated flange, which is the termination of the externally visible ventral plate mentioned under 19.

20 When the petiole is disarticulated from the gaster, the petiole sternite, in posterior view, is revealed as a complex structure. In the posterior third of its length the sternite bifurcates into an externally visible ventral plate and an internally projecting sclerite that terminates in a concave arc, which forms the actual articulation with the helcium; this is not visible in normally mounted specimens. Within Ponerini this specialised structure has also been detected only in *Phrynoponera* and to a somewhat lesser extent in those species of *Pachycondyla* which formerly constituted the genus *Brachyponera*. The morphology is currently suspected to have developed independently in each case and is not a synapomorphy of the three, or of any two of the three, but this awaits proof. The internal part of the sclerite corresponds to the normal articulatory surface seen in other Ponerini; the outer plate that conceals it is the secondary development.

21 and 22 In anterior view the helcium has a narrow crest of cuticle between the ventral apices of the arched tergite. There appear to be two possible origins for this crest. One possibility is that a ridge of cuticle has arisen *de novo* from the first gastral sternite adjacent to the helcium and anterior of the prora. Alternatively, this crest could be the remnant of the original prora and the sternal structure that now appears to be the prora is really a secondary development. Reduction and insertion of the prora between the apices of the helcium tergite also occurs in *Phrynoponera* and *Brachyponera*. However, in both these groups the inserted cuticle apparently represents the remnants of the prora itself, which is otherwise entirely absent from the sternum. *Asphinctopone* retains a large, externally visible prora that appears to be genuine and not a secondary structure that developed after the reduction of the original prora and its insertion between the apices of the helcium tergite. Based on these comparisons, the first option appears more likely, but in either case the combined structure of the helcium and prora appears to be a unique development of *Asphinctopone*.

23 The complete lack of presclerites on both tergite and sternite of abdominal segment IV (second gastral segment) means that there is no trace of a girdling constriction on the segment. The disappearance of presclerites, and of the constriction, is certainly an apomorphy by reduction.

24 In most genera of Ponerini a stridulitrum is generally universally absent or universally present. A polymorphic condition for this character occurs in *Pachycondyla*, but that genus is certainly polyphyletic as presently understood and much in need of a detailed analysis.

Characters 6 and 23 immediately and very obviously separate *Asphinctopone* workers from all other members of the *Pachycondyla* group of genera. Characters 21 and 22 together are unique to the genus, and the second halves of characters 4 and 8 also appear unique. Characters 1 – 24 together form an inclusive diagnosis that isolates *Asphinctopone* from all other genera in the tribe.

In general appearance *Asphinctopone* species resemble small members of the *melanaria*-group of *Pachycondyla*, which are those species that formerly constituted most of the genus *Mesoponera*. However, *melanaria*-group species can be distinguished by the following characters: the mandible is triangular to elongate-triangular and not oblique; the mandible has more than 6 teeth on the apical margin and lacks a tooth-like process on the basal margin; the apical antennomere is not hypertrophied; the clypeus is simple; the promesonotal suture is not deeply impressed nor cross-ribbed; the mesotibiae and metatibiae each have two spurs; the petiole sternite has a simple posterior structure; the helcium and prora are not modified as described above; and presclerites are present on the second gastral segment (= abdominal segment IV).

Male: unknown.

Synonymic synopsis of species

differentens Bolton & Fisher **sp. n.**

silvestrii Santschi, 1914

= *lucidus* Weber, 1949 **syn. n.**

= *lamottei* (Bernard, 1953) **syn. n.**

Key to species (workers)

- 1 With propodeum in profile the dorsum with pubescence extremely scanty, almost absent. Side of propodeum with scattered punctures, the spaces between them usually smooth (Fig. 2a,c). (Guinea, Ivory Coast, Ghana, Nigeria, Cameroun, Gabon, Central African Republic)..... *silvestrii*
- With propodeum in profile the dorsum with a pelt of erect, weakly curved pubescence. Side of propodeum entirely densely irregularly sculptured (Fig. 2b,d). (Central African Republic) *differentens*

Species of *Asphinctopone*

Asphinctopone silvestrii Santschi

(Figs 1a,b; 2a,c)

Asphinctopone silvestrii Santschi, 1914: 318, fig. 6. Holotype worker, NIGERIA: Olokemeji, xii. 1912 (*F. Silvestri*) (not in DEUN or NHMB, presumed lost; see note).

Asphinctopone lucidus Weber, 1949: 7, figs. 5–7. Holotype worker, CENTRAL AFRICAN REPUBLIC (= “Fr. Equat. Africa” on data label): Ubangi-Shari, Bas Mbomu, 5 mi. W. of Bangassou, 12.iii.1948, #2210 (*N.A. Weber*) (AMNH) [examined]. **Syn. n.**

Lepidopone lamottei Bernard, 1953: 208, fig. 4. Holotype worker, GUINEA: 22. Nyon For. (= Nion, Mt. Nimba), 10.1.8/2 (*Lamotte*) (MNHN) [examined]. **Syn. n.** [Combination in *Asphinctopone* by Brown, 1953: 3.]

Note. Conversations between Bruno Spinosa (DEUN) and Fabrizio Rigato (MSNM), as reported to Barry Bolton, have established that the holotype of *A. silvestrii* cannot be found in the Silvestri collection in Naples. Daniel Burckhardt (NHMB) informs us that the *silvestrii* holotype has never been in the Santschi collection.

Worker. TL 3.3 – 3.6, HL 0.78 – 0.83, HW 0.62 – 0.68, CI 78 – 83, SL 0.53 – 0.63, SI 85 – 93, PW 0.44 – 0.49, WL 0.96 – 1.06 (20 measured).

Mandible smooth and shining, unsculptured except for a few pits from which hairs arise. Eye small, maximum diameter 0.04 – 0.06 (OI 6 – 9), of only 5 – 8 poorly defined ommatidia. No distinct carina present between eye and base of mandible but a fine, weak cuticular crest present laterally that extends from the base of the mandible to above the eye, and terminates just behind the level of the eye. In full-face view posterior margin of head very shallowly convex. In the same view the scape, when laid straight back from its insertion, just fails to reach, to fractionally exceeds, the posterior margin. Dorsal surface of frontal lobes more strongly sculptured than remainder of head. Dorsum of head finely minutely punctulate; sides behind and below eyes with widely scattered, slightly larger punctures, the spaces between them smooth and shining. Promesonotal suture with short cross-ribs on the anterior margin of the mesonotal section. In profile the promesonotal suture and metanotal groove are both narrow and deeply impressed, so that the relatively short mesonotum forms a distinct, isolated convexity between them. Base of metanotal groove with short cross-ribs. Sulcus between mesonotum and mesopleuron present, the latter also with a transverse sulcus that divides it into anepisternum and katepisternum. Propodeal outline in profile slightly variable in shape: length and slope of dorsum shows variation, as does the degree of convexity of the dorsum and posterior angle, and the convexity of the poste-

rior face, which varies from straight to very weakly convex. Propodeum unarmed and the small propodeal spiracle is low down on the side. Dorsum of pronotum and mesonotum sparsely sculptured with scattered small punctures, the density of the punctures weakly variable between individuals; punctures on propodeal dorsum more coarse. Side of propodeum with scattered punctures, the spaces between them generally smooth but sometimes with faint traces of interstitial sculpture; propodeal declivity unsculptured, weakly marginate laterally. Legs relatively short, maximum length of hind femur 0.60 – 0.67. Petiole surmounted by an unsculptured high, narrow scale that is convex dorsally (petiole maximum height 0.52 – 0.58; maximum thickness of scale in profile 0.14 – 0.18); scale in dorsal view broad (maximum width 0.36 – 0.39). Petiole with a short posterior peduncle that is equipped dorsally with three strong transverse carinae; rarely there is a trace of a fourth carina posteriorly. Subpetiolar process complex, as discussed above. First and second gastral tergites with small punctures, those on the second tergite usually somewhat more dense than on the first; spaces between punctures smooth and shining. Setae sparsely present on clypeus, very dense on pygidium and hypopygium, but otherwise all dorsal surfaces of head, mesosoma, petiole and gaster lack setae. Ventral surface of head with 1 – 2 short setae present, and a few on gastral sternites 1 – 3. Scapes, femora and tibiae have fine appressed pubescence but completely lack standing setae. Dorsal surfaces of head and mesosoma with sparse appressed pubescence, especially scanty on the dorsal propodeum where it is almost absent. Colour of individuals varies from reddish yellow to reddish brown.

Queen. TL 3.8, HL 0.79, HW 0.64, CI 81, SL 0.56, SI 88, PW 0.52, WL 1.08.

Slightly larger but otherwise very similar to the worker, with cephalic measurements falling within the same range. The extra size is accounted for by the mesosoma, which has a full set of flight sclerites, and a slightly larger gaster. Transverse sulcus on mesopleuron is more strongly developed than in worker. Head with three ocelli present; eye distinctly larger than in worker, its maximum diameter 0.16 (OI 25). Known from only a single dealate specimen (BMNH).

Following the initiation of the genus and its type-species *silvestrii* by Santschi (1914), two other specimens collected by subsequent authors were also described as new species, *lucidus* and *lamottei*. Each of these is based on single specimens, as was *silvestrii*. The two later authors apparently relied only on published descriptions and never examined type-specimens. Although none of the descriptions was very detailed, they indicated that the three nominal taxa were extremely closely related and probably synonymous. The loss of the earliest of the three holotypes grouped here makes direct comparison impossible now, but an overview of all the material that is available, and its comparison with the two surviving holotypes and the description of the missing holotype, confirms that only a single species is represented.

Weber's description and figures of *A. lucidus* indicate nothing to separate it from the mass of material examined, except for his comment that the scapes are longer than in *silvestrii*. In the material examined, the scapes, when laid straight back from their insertions in full-face view, range in length from just failing to reach the posterior margin of the head to just exceeding the margin, with intermediate lengths present. Small changes in the orientation of the head make the scapes appear to extend to different distances. Weber's fig. 5 shows the scapes crossing the lateral margin of the head just in front of the posterior corners. This also occurs in other material when the scapes are oriented similarly. Therefore Weber's assertion that the scapes of *lucidus* are longer is incorrect; he was merely comparing his specimen with a drawing that did not have the same orientation. Measurement of the holotype of *lucidus* confirmed this as its SI of 93, although at the upper end of the measured range, is frequently duplicated throughout the species, and every SI from 85 to 93 has been recorded.

A Nigerian specimen from Gambari, not far from the *silvestrii* type-locality of Olokemeji, matches Santschi's description in all respects except colour; it is a somewhat darker reddish brown. This specimen, in turn, is indistinguishable from the holotype of *lamottei* and from the other material examined.

All examples of this species were retrieved from samples of leaf litter or topsoil, or in the rotting trunks of fallen trees, small pieces of dead wood, a rotting banana stem on the forest floor, and once from a termitary.

Material examined. **Guinea:** Mt Nimba, Nion (*Lamotte*). **Ivory Coast:** Forêt de Teke, Anyama (*T. Diomande*); Ndouci, Nzi Noua (*W.L. Brown*); Lamto, Toumodi (*J. Levieux*); Lamto (*K. Yeo*); Adiopodoumé, nr Abidjan (*I. Löbl*). **Ghana:** Bunso (*R. Belshaw*); Eastern Bunso (*R. Belshaw*); Ofinso (*R. Belshaw*). **Nigeria:** Gambari (*B. Bolton*). **Cameroun:** Ebodjie (*A. Dejean*); Mbalmayo (*N. Stork*); Nkoemvon (*D. Jackson*); Prov. Sud-Ouest, Korup N.P., NW Mundemba (*B.L. Fisher*); Prov. Sud, N'kolo, Bondé For., SSE Elogbatindi (*B.L. Fisher*); Res. de Faune de Campo, ESE Ébodjé (*B.L. Fisher*); Res. Campo, Massif des Mamelles (*B.L. Fisher*). **Gabon:** Prov. Woleu-Ntem, ESE Minvoul (*B.L. Fisher*); Prov. Estuaire, F.C. Mondah, NNW Libreville (*B.L. Fisher*). **Central African Republic:** Ubangi-Shari, Bas Mbomu, Bangassou (*N.A. Weber*); P.N. Dzanga-Ndoki, Lidjombo (*B.L. Fisher*).

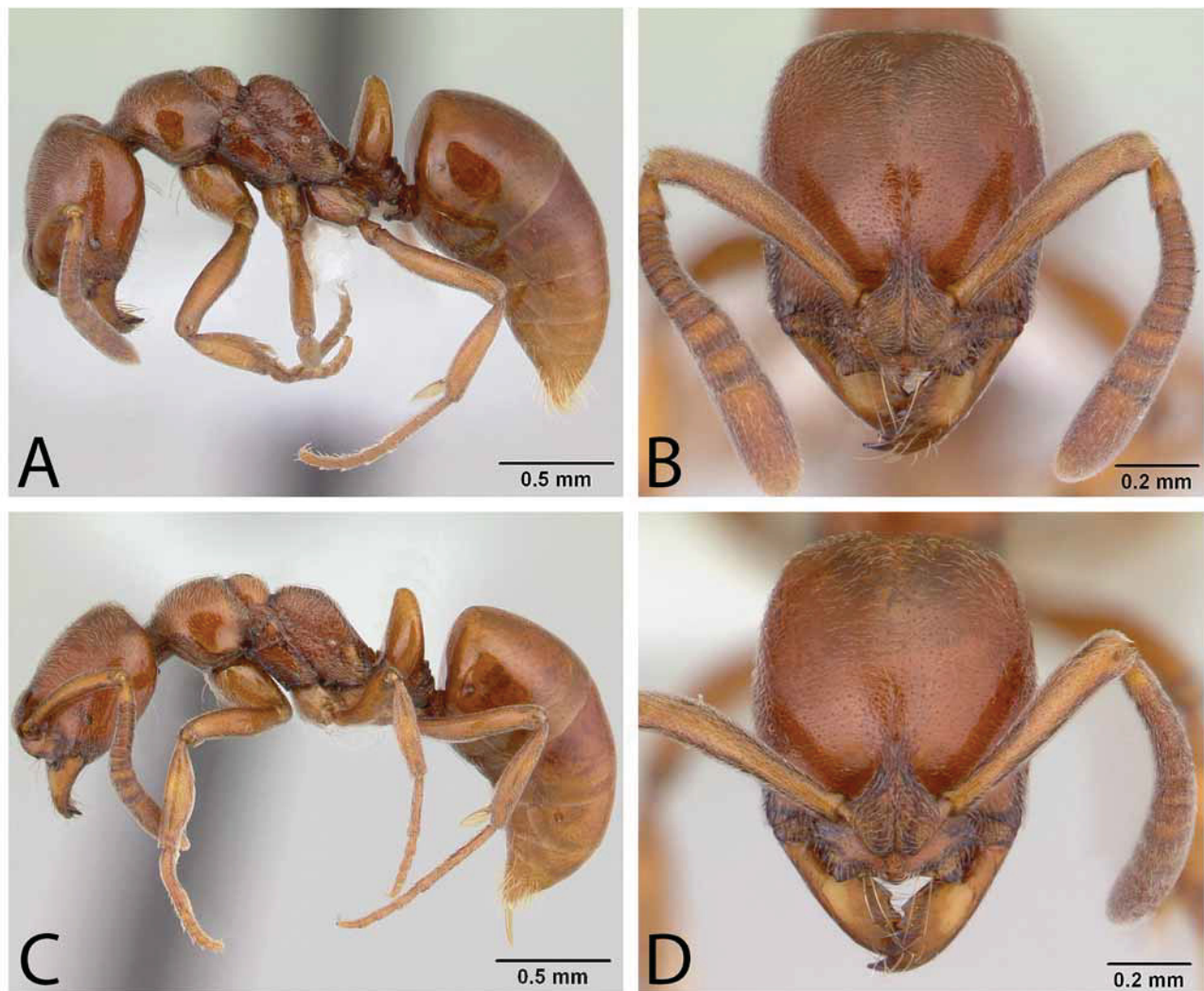


FIGURE 1. *Asphinctopone* spp. full face and lateral view. A–B, *silvestrii* worker, CASENT0178222; C–D, *differens* holotype worker CASENT0417143.

***Asphinctopone differens* Bolton & Fisher sp. n.**
(Figs 1c,d; 2b,d)

Holotype worker. TL 3.7, HL 0.82, HW 0.66, CI 81, SL 0.61, SI 92, PW 0.48, WL 1.06. Answering the description of *silvestrii*, above, but differing as follows.

Side of propodeum entirely densely irregularly sculptured.

Dorsum of propodeum with a pelt of fine short pubescence that is erect and weakly curved.

In addition, pubescence on the pronotum and mesonotum is more dense and more elevated than in *silvestrii*. The propodeal dorsum in profile is longer and flatter than in any *silvestrii* specimen examined, but the latter shows variation in the shape of the propodeum, and as only a single specimen of *differens* is known it is impossible to tell if the sclerite also shows variation here. In *differens* the dorsal margin of the anepisternum is distinctly concave, whereas in all known *silvestrii* specimens it is flat to very feebly sinuate.

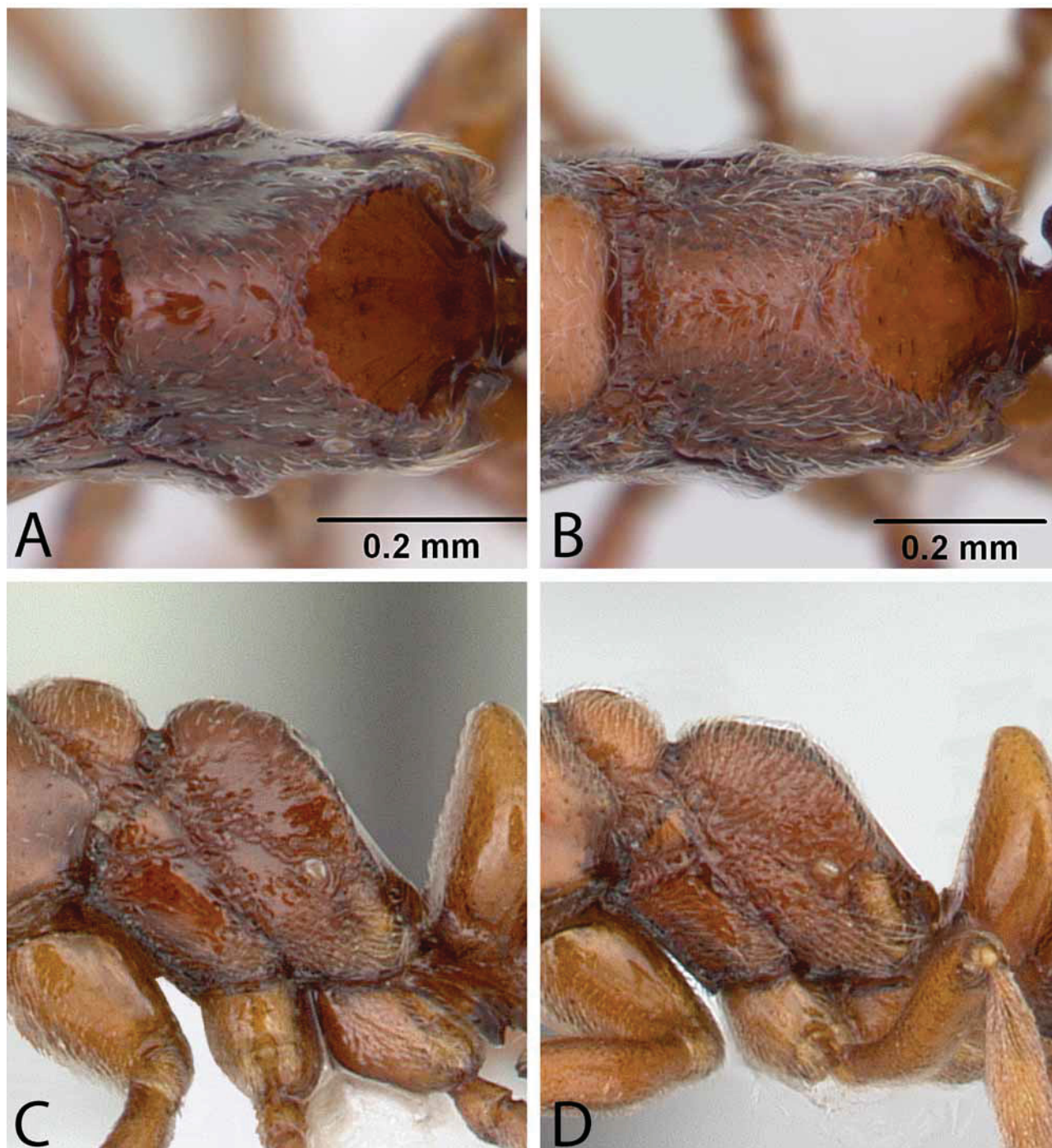


FIGURE 2. *Asphinctopone* spp. dorsal and lateral view of propodeum. A, C, *silvestrii* worker, CASENT0178222; B,D, *differens* holotype worker CASENT0417143. Note differences in pilosity and sculpture.

Holotype worker, **Central African Republic**: P.N. Dzanga-Ndoki, 37.9 km. 169°S Lidjombo, 2°22'N, 16°10'E, 360 m., 21.v.2001, #4130(30), CASENT 0417143, sifted litter, rainforest (*B.L. Fisher*) (CASC).

The two species are obviously very closely related. We infer they are two distinct species because (1) specimens of *silvestrii* are known from the type-locality of *differens* and thus occur in sympatry and (2) the differences between the single specimen of *differens* and all the observed material of *silvestrii* are distinct for multiple non-overlapping characters

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References

- Belshaw, R. & Bolton, B. (1994) A survey of the leaf litter ant fauna in Ghana, West Africa. *Journal of Hymenoptera Research*, 3, 5–16.
- Bernard, F. (1953) La réserve naturelle intégrale du Mt Nimba. 11. Hyménoptères Formicidae. *Mémoires de l'Institut Français d'Afrique Noire*, 19 (1952), 165–270.
- Bolton, B. (2003) Synopsis and classification of Formicidae. *Memoirs of the American Entomological Institute*, 71, 1–370.
- Brown, W.L., Jr. (1953) Characters and synonymies among the genera of ants. Part 2. *Breviora*, 18, 1–8.
- Brown, W.L., Jr. (1976) Contributions toward a reclassification of the Formicidae. Part 6. Ponerinae, tribe Ponerini, subtribe Odontomachiti. Section A. Introduction, subtribal characters, genus *Odontomachus*. *Studia Entomologica* (N.S.), 19, 67–171.
- Dejean, A., Durand, J.L. & Bolton, B. (1996) Ants inhabiting *Cubitermes* termitaries in African rain forest. *Biotropica*, 28, 701–713.
- Ouellette, G.D., Fisher, B.L. & Girman, D.J. (2006) Molecular systematics of basal subfamilies of ants using 28S rRNA. *Molecular Phylogenetics and Evolution*, 40, 359–369.
- Santschi, F. (1914) Formicides de l'Afrique occidentale et australe du voyage de Mr. le Professeur F. Silvestri. *Bollettino del Laboratorio di Zoologia generale e agraria della R. Scuola superiore d'Agricoltura in Portici*, 8, 309–385.
- Weber, N.A. (1949) New ponerine ants from Equatorial Africa. *American Museum Novitates* 1398, 1–9.